THE COMPARATIVE MORPHOLOGY OF THE COCHLOSPERMACEAE. III. THE FLOWER AND POLLEN[1]

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ABSTRACT

The flowers and pollen of *Amoreuxia* and *Cochlospermum* have been studied anatomically to contribute to determining trends of specialization and relationships of the Cochlospermaceae. Perianth vascularization consists of 10 traces in some species of *Cochlospermum* but is reduced to 6 or 5 in other species. Androecial development is centrifugal with the vascularization consisting of 5 or more trunk bundles. The ovary has a single, 3–5 carpellate, ramified locule in all species examined. Pollen is mostly intectate to semitectate and tricolporoidate. Floral morphology of *Bixa* is more specialized in some ways and less specialized in others and its placement in a separate family from *Amoreuxia* and *Cochlospermum* can be justified. While the Cochlospermaceae show similarities to many parietalian families, the floral anatomy is also compatible with that found in the Malvales.

Previous papers in this series (Keating, 1968, 1970), discussed the relationships of the Cochlospermaceae using the evidence from vegetative anatomy. Although floral and pollen morphology have demonstrated value in systematics, there is no complete treatment of the flower of even a single species of *Cochlospermum*. The genus *Amoreuxia* is not known to have been anatomically investigated at all. Schnarf (1931) investigated the development of the seed of *C. orinocense*. His comments on the nature of the septa of the gynoecium made no mention of its vascular anatomy. In illustrating the vasculature of the perianth and androecium of *C. vitifolium*, Wilson (1937) pointed out that more species would have to be investigated before drawing conclusions regarding the basic nature of the vasculature in this genus. The numerous stamens and reported parietal placentation have placed the family in the Bixales-Flacourtiaceae alliance (Cronquist, 1968; Takhtajan, 1969), while vegetative anatomy (Keating, 1968, 1970) indicates malvalian affinities.

Erdtman (1952) briefly described the pollen of three species of *Cochlospermum* and noted their resemblance to pollen of *Bixa*. Nair (1962) briefly described the pollen of *C. religiosum*. Floral anatomy and pollen of *Rhopalocarpus*, previously assigned to the Cochlospermaceae, has been investigated by Huard (1965*a*, *b*, *c*).

My present purpose is to examine the floral anatomy and pollen of many species of Cochlospermaceae in order to determine more accurately the relationships of the family.

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TABLE 1. Specimens examined[a].

Name	Collector, source[b]	Material
Amoreuxia wrightii A. Gray	*von Rozynski s.n.* (1932), F	Bud
	Webster & Miller 13137, PUL	Bud
	Wooten s.n. (1919), US	Bud
	Axtell F-03484, SIUE	Pollen
A. *palmatifida* Mocino & Sesse	*Niles 425*, ARIZ	Bud
Bixa orellana L.	*Tate 32*, NY	Bud
	Keating 360, 414, SIUE	Bud, pollen
Cochlospermum fraseri Planch.	*Specht s.n.* (1948), US	Bud
	Perry s.n. (1949), US	Bud
C. *gillivraei* Benth.	*Sprecht s.n.* (1948), US	Bud
C. *gregorii* F. Muell.	*Perry s.n.* (1948), US	Bud, pollen
C. *orinocense* Steud.	*Kuhlmann & Jimbo 387*, SP	Bud, pollen
	Holt & Gehringer s.n. (1930), US	Bud, pollen
	Piras s.n. (1947), US	Bud, pollen
C. *parkeri* Planch.	*Klug s.n.* (1933), US	Bud
C. *planchonii* Hook. f. *ex* Planch.	*Wimbush s.n.* (1962), SIUE	Bud
	Chevalier s.n. (1910), P	Bud
	Ibem s.n. (1963), SIUE	Pollen
C. *regium* (Mart & Shrank) Pilger	*Hoehne s.n.* (1931), SP	Bud
	Hassler s.n. (1907–8), US	Bud
	Dahlgren s.n. (1935), F	Pollen
C. *religiosum* (L.) Alston *ex* Trimen	*Subba Rao s.n.* (1963), CAL	Bud
	Bole s.n. (1963), BLAT	Bud, pollen
	Yongboonkird s.n. (1963), BK	Bud
C. *tetraporum* H. Hallier	*Pflanz 4034*, US	Bud
C. *tinctorium* A. Rich	*Chevalier 94*, P	Bud
	Le Testu s.n. (1922), P	Pollen
C. *vitifolium* (Willd.) Spreng.	*Stern, Eyde & Ayensu 1694*, US	Bud
	Rowlee & Mixter s.n. (1921), US	Bud
	Jack s.n. (1930), US	Bud
	Schipp 49, NY	Pollen
C. *williamsii* Macbride	*Williams* (1929), F	Bud

[a] Specimens cited according to the procedure recommended by Stern and Chambers (1960).
[b] Southern Illinois University, Edwardsville, designated as SIUE.

MATERIALS AND METHODS

Flowers and buds of *Amoreuxia* and *Cochlospermum* from a geographically diverse sampling of each genus were obtained for study (Table 1). Specimens of *Bixa* were available for comparison. Floral anatomy was studied from microtomed serial sections and from cleared thick sections of both dried and FPA preserved material. Thick sections were cleared using the NaOH-Chloral hydrate method of Arnott (1959) or the peroxide-lactic acid technique of Sporne (1948). Occasionally 5% sodium hypochlorite (straight household bleach) was needed to remove dark deposits from the floral receptacle. Vascular structure of the clearings was readily visible without staining and drawings were made with the aid of a 50× dissecting microscope. Serial microtomed sections of most species were prepared using paraffin techniques from preserved material or from dried herbarium specimens. Staining was accomplished using Safranin O and Fast Green FCF for the preserved material while Methyl Violet 2B and Bismarck Brown Y proved to be the best combination for the restored material.

Pollen was prepared by KOH-acetolysis (Faegri & Iversen, 1964) and mounted in glycerin jelly containing safranin. Sections of some samples were made at 1 μ thickness with an ultramicrotome after embedding in Epon-Araldite. Measurements of polar and equatorial axes were based on at least 20 grains per sample from acetolyzed specimens.

Descriptions of floral anatomy emphasize vascularization because of its demonstrated value in determining relationships (Moseley, 1967). Descriptions of vascular "events" in the observations section are topographical and are designed for comparisons of the anatomy of mature flowers. Such terms as "diverge from the stele" refer to the appearance of vascular bundles viewed in successively higher (more distal) serial sections and yield the most efficient graphic descriptions. It should be understood that developmental interpretations of these terms will produce nonsense.

OBSERVATIONS

General floral morphology and histology is similar for both *Cochlospermum* and *Amoreuxia*. The perianth is composed of five quincuncially imbricate sepals alternating with five rotate petals. Both genera show a tendency toward zygomorphy, the condition being more pronounced in *Amoreuxia*. The bright orange-yellow petals in both genera have red glide ways on four of the five petals. These are only slightly visible on fresh flowers of *C. vitifolium*. Short unbranched trichomes range from dense to nearly absent on the receptacle and sepals. Vascularization enters the receptacle as a siphonostele and extraxylary fibers are absent at anthesis. In some specimens of *Cochlospermum* and *Amoreuxia*, vertical lysigenous canals are present in the ground tissue.

Vascularization of the perianth is most discrete in *Cochlospermum orinocense*, *C. gregorii*, and *C. regium*. In these species the vasculature of the calyx consists of five vascular bundles which diverge from successively higher serial sections in a ⅖ phyllotactic sequence. Each sepal is vascularized by one of these bundles (Fig. 29). At higher levels they trifurcate with the lateral branches fusing to form a ring (Fig. 10). At the base of the sepals, this ring of vasculature is used up in producing a series of parallel veinlets in each sepal. Alternating with the five sepal traces, five petal traces leave the siphonostele above them (Figs. 10, 29). At higher levels, the petal traces also appear to branch to form numerous parallel bundles in the petals. In *Amoreuxia, C. vitifolium*, and in most other species of *Cochlospermum* examined, the perianth traces are five to six instead of 10 in number. The traces diverge from the siphonostele in no discernible phyllotactic pattern. In higher sections, where the receptacle is considerably broadened, the traces trifurcate with the lateral branches fusing with neighboring laterals to form a circular vascular plexus (Figs. 2–3, 9, 31). Vascular bundles continue upward from the original traces and vascularize the sepals. Traces originating from the plexus between the original sepal traces vascularize the petals.

The androecium.—The stamens have basifixed anthers which are four loculed. Pollen is shed through single introrse apical pores and a pair of lateral basal pores in most species of *Cochlospermum* (Figs. 4–6). In *Amoreuxia*, the anthers have a
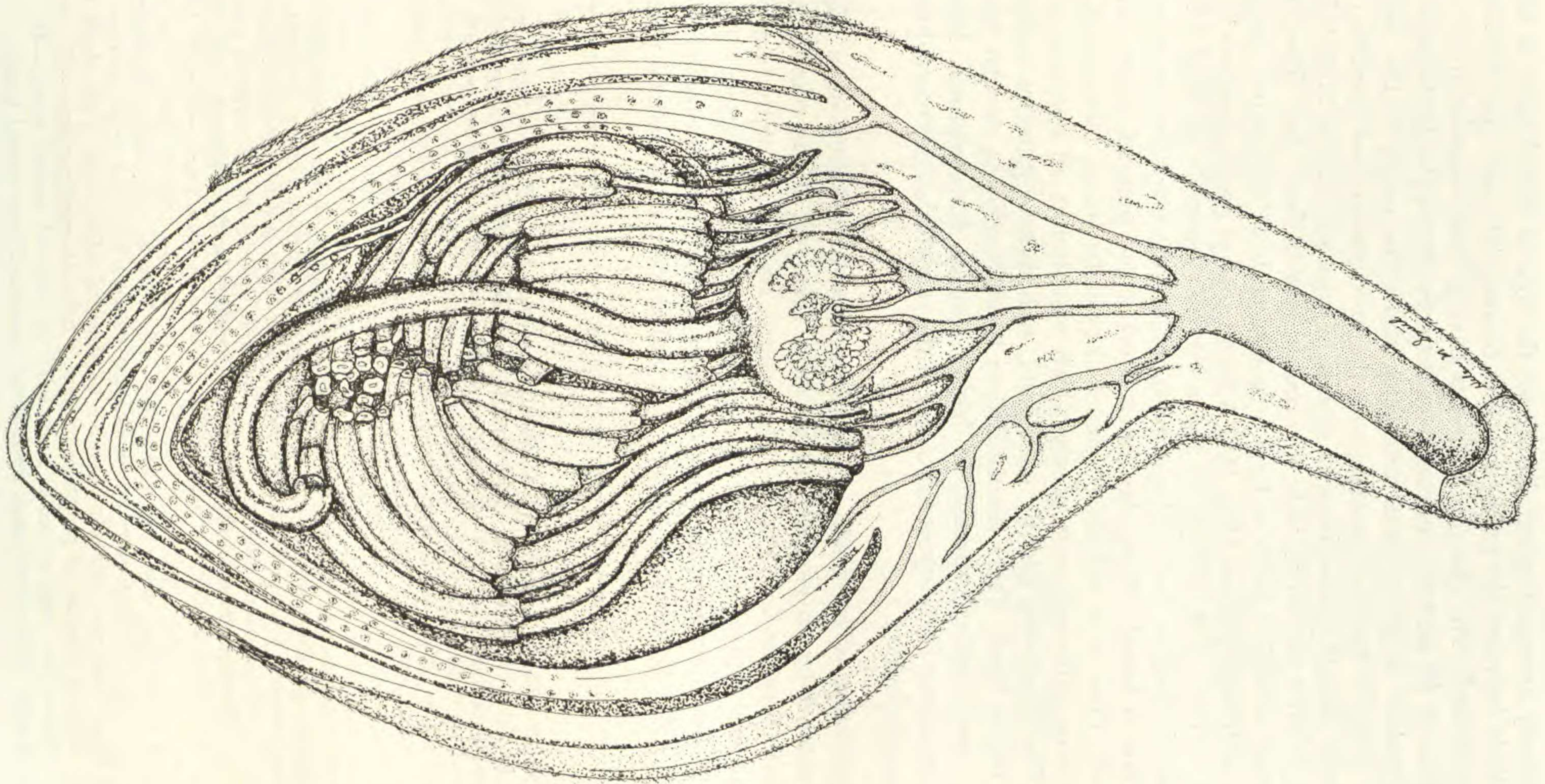
FIGURE 1.—Longisection of flower of *Cochlospermum vitifolium*, × 6.5. Cut was made along plane of bilateral symmetry. Note differences in length of anther filaments, the recurved style, the curved peduncle.

pair of obliquely arranged apical slits across the tops of lateral pairs of locules (Fig. 7). Septa between the pairs of locules become thin and may disintegrate when pollen is shed. The elongate filaments have a single vascular trace which enters the base of the anthers and continues between the locules to the apex.

Vascularization of the stamens originates above the origin of the perianth vasculature with 5–6 traces alternating with the previous series of bundles (Figs. 2–3). As many as 8–10 stamen bundles appear in some species due to early bi- or trifurcation, but five gaps in the stele are common even in these cases. These trunk bundles branch at higher levels to form a broken circle of vasculature which develops in a centrifugal pattern (Fig. 11). A broad zone of stamen traces is formed which at the surface of the receptacle appears to be a complete circle of 3–6 concentric ranks of bundles. In *Cochlospermum gregorii* the most obscure pattern of vascularization is found. From the lowest level where perianth traces diverge from the stele, there is an indistinct number of vascular traces, bifurcations, and fusions forming a discontinuous plexus which vascularizes all segments of the perianth. The remaining, slightly contracted, siphonostele provides androecial traces at a higher level. There are no distinct trunk bundles; a circular band of vasculature moves out centrifugally as higher sections are examined. Rows of stamen traces mature first nearest the center of the receptacle, the outermost being the most recently formed.

The gynoecium.—The pistil of Cochlospermaceae consists of a globose ovary surmounted by an elongate, linear style, recurved at the summit in the plane of bilateral symmetry (Fig. 1). The ovary is three, four, or five carpellate, and all specimens showed the same anatomy with minor modifications. Transections through the lower or upper parts of the ovary give the appearance of axile placentation while, transections through the middle part show parietal placenta-

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FIGURES 2–18.—Floral anatomy of Cochlospermaceae.—2–3. Cleared transverse thick sections through floral receptacle.—2. *Amoreuxia palmatifida*, × 10. Note five perianth traces and six stamen trunk bundles.—3. *Cochlospermum vitifolium*, × 5. Note six perianth traces and five stamen trunk bundles.—4–7. Cleared whole anthers, × 6.—4. *Cochlospermum vitifolium*, adaxial view. Note small apical pore.—5. *Cochlospermum religiosum*, lateral and adaxial views. Note basal pore in lateral view and elongate apical pore in adaxial view.—6. *Cochlospermum religiosum*, adaxial view. Note large apical pore.—7. *Amoreuxia palmatifida*, lateral and adaxial views. Note pair of elongate apical slits.—8. *Cochlospermum religiosum*, × 7. Longisection of ovary showing placental ridges.—9–10. Diagrammatic composite longisections showing perianth vasculature types.—9. Perianth traces trifurcate with lateral branches fusing to form a plexus from which petal traces and lateral sepal traces arise, e.g. *Amoreuxia, Cochlospermum vitifolium*.—10. Perianth vascularized by separate petal and sepal traces, e.g. *Cochlospermum orinocense*.—11. *Cochlospermum religiosum*, × 9. Stamen trunk bundles and anastomosing branches which produce stamen traces.—12–18. *Cochlospermum regium*, × 7. Serial transections through the pistil.—12. View at level of receptacle. Note three dorsal bundles and three ventral bundles.—13. View of ovary above the receptacle, appears trilocular.—14. View of ovary cut equidistant between base and upper surface. Note parietal placentation with pairs of ventral bundles in placental ridges.—15. View above center of ovary.—16. View at juncture of placentae to form a trilocular configuration.—17. View at base of style. Note stylar canal at center surrounded by pairs of ventral traces.—18. View through center of style. Note stylar canal, three dorsal traces and three ventral traces.
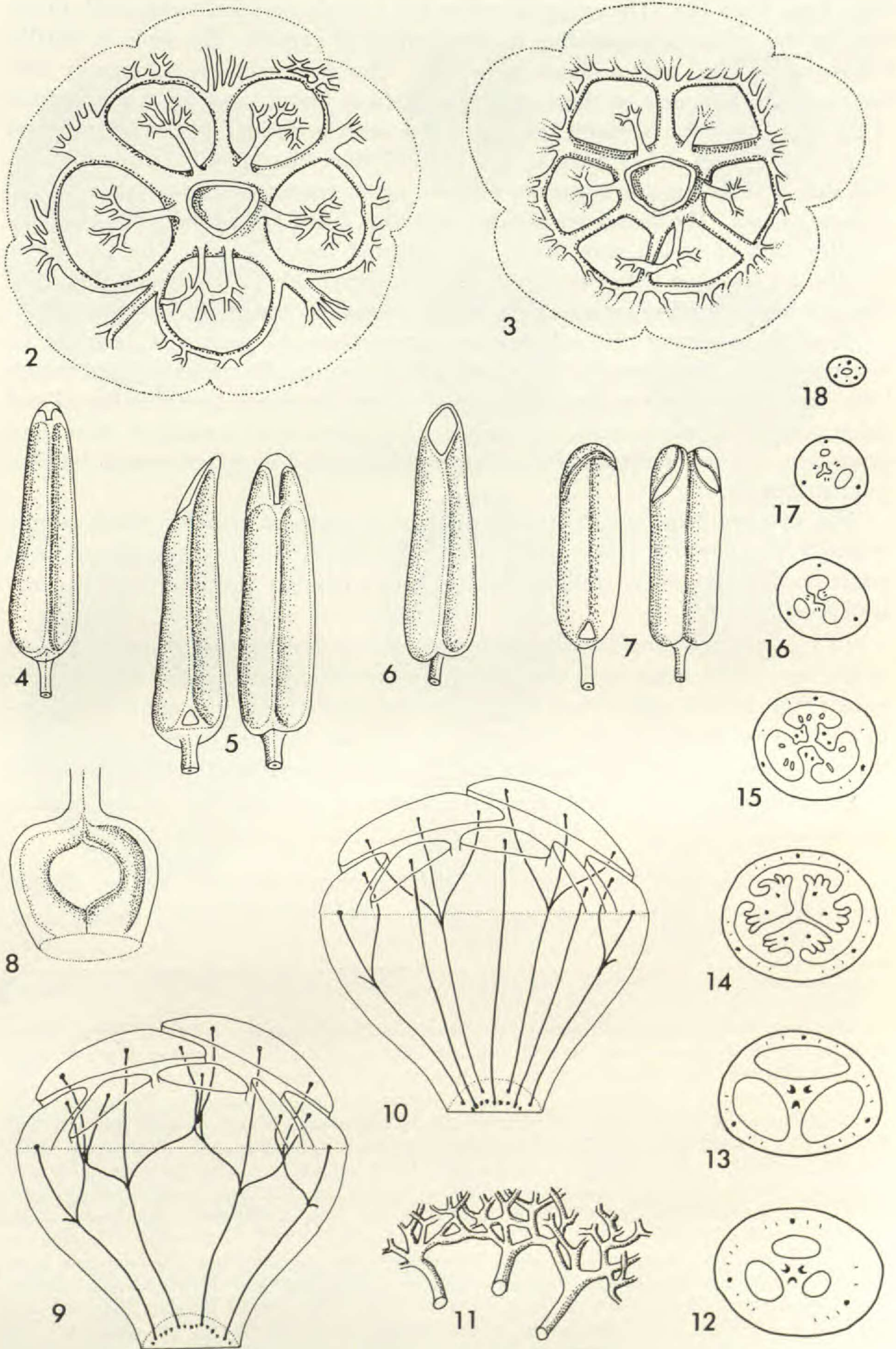
tion (Figs. 8, 12–18). The ovary therefore has a single ramified locule with three, four, or five lobes corresponding to the number of carpels. The style is usually hollow and is lined with a glandular surface. The stylar canal is not usually continuous with the locule of the ovary. The pistil is vascularized by what remains of the stele above the perianth and androecial vascularization. In *Cochlospermum gregorii*, *C. fraseri*, *C. religiosum*, and *C. vitifolium*, the pistil is five carpellate. The stele divides into ten segments with five outer segments alternating with five inner segments. The five inner bundles represent fused lateral pairs of carpellary bundles each of which may divide into pairs at higher levels. The five inner bundles are inverted with the phloem on the adaxial side of the xylem (Fig. 30). The outer five bundles represent the dorsal carpellary traces.

In other specimens of *Cochlospermum orinocense*, *C. parkeri*, *C. regium*, *C. tetraporum*, *C. tinctorium*, *C. williamsii*, and *A. wrightii*, the pistil is three-carpellate. Vascularization is as described above except that there are three dorsal and three pairs of ventral traces. Specimens of *C. planchonii* examined were four carpellate, and one specimen of *C. religiosum* had only four sets of ventral bundles but five carpels.

The connate carpel walls are vascularized by pairs of bundles which supply traces to the placental ridges and ovules. The dorsal bundles may disappear at lower levels of the ovary wall by dividing into a number of minor parallel ovary wall bundles.

In a specimen of *Cochlospermum regium*, the ventral bundles are quite distinct in the base of the ovary with the phloem on the adaxial side of the three bundle pairs (Figs. 12–13). The dorsal bundles at that level branch into numerous traces to the ovary wall but are not used up in the process. At the top of the ovary, the three fused pairs of ventral bundles and the three dorsal bundles vascularize the length of the style as six evenly distributed traces (Fig. 18). The ventral bundles appear as free pairs only in the central portion of the ovary (Figs. 14–16).

Pollen.—Grains of *Amoreuxia* and *Cochlospermum* are quite similar. Shape: mostly spheroidal to subprolate, occasionally suboblate. Structure: mostly semi-

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FIGURES 19–31.—Photomicrographs of pollen and floral anatomy.—19–28. Pollen grains of Bixaceae, Cochlospermaceae, × 1000.—19–20. *Bixa orellana.*—19. Equatorial view. Note reticulate ektexine, sculpturing elements on colpus, pore with constricted lateral extensions.—20. Equatorial view. Note oval pore.—21–22. *Cochlospermum religiosum.*—21. Equatorial view. No visible pore.—22. Polar view, note finely reticulate ektexine.—23–24. *Cochlospermum tinctorium.*—23. Equatorial view. Note equatorial constriction in colpus.—24. Polar view. Note intectate, rugulate sculpturing.—25. *Amoreuxia wrightii*, equatorial view. Note constriction in colpus at equator.—26. *Cochlospermum parkeri*, equatorial view. No pore is visible in colpus.—27–28. *Cochlospermum gregorii.*—27. Equatorial view. Note constricted colpus.—28. Polar view. Note reticulate ektexine, sharply defined ends of colpi.—29–31. Transections through the floral receptacle showing vasculature.—29. *Cochlospermum orinocense*, × 10. Note five large sepal traces and five petal traces (arrows).—30–31. *Cochlospermum vitifolium.*—30. Gynoecium vasculature below surface of the receptacle, × 45. Note dorsal bundles (arrows) and fused ventral bundles (Vb) with xylem on the abaxial side.—31. Section cut above level of origin of androecial vascularization, × 10. Note perianth traces; note three simple and two branched stamen trunk bundles (arrows).
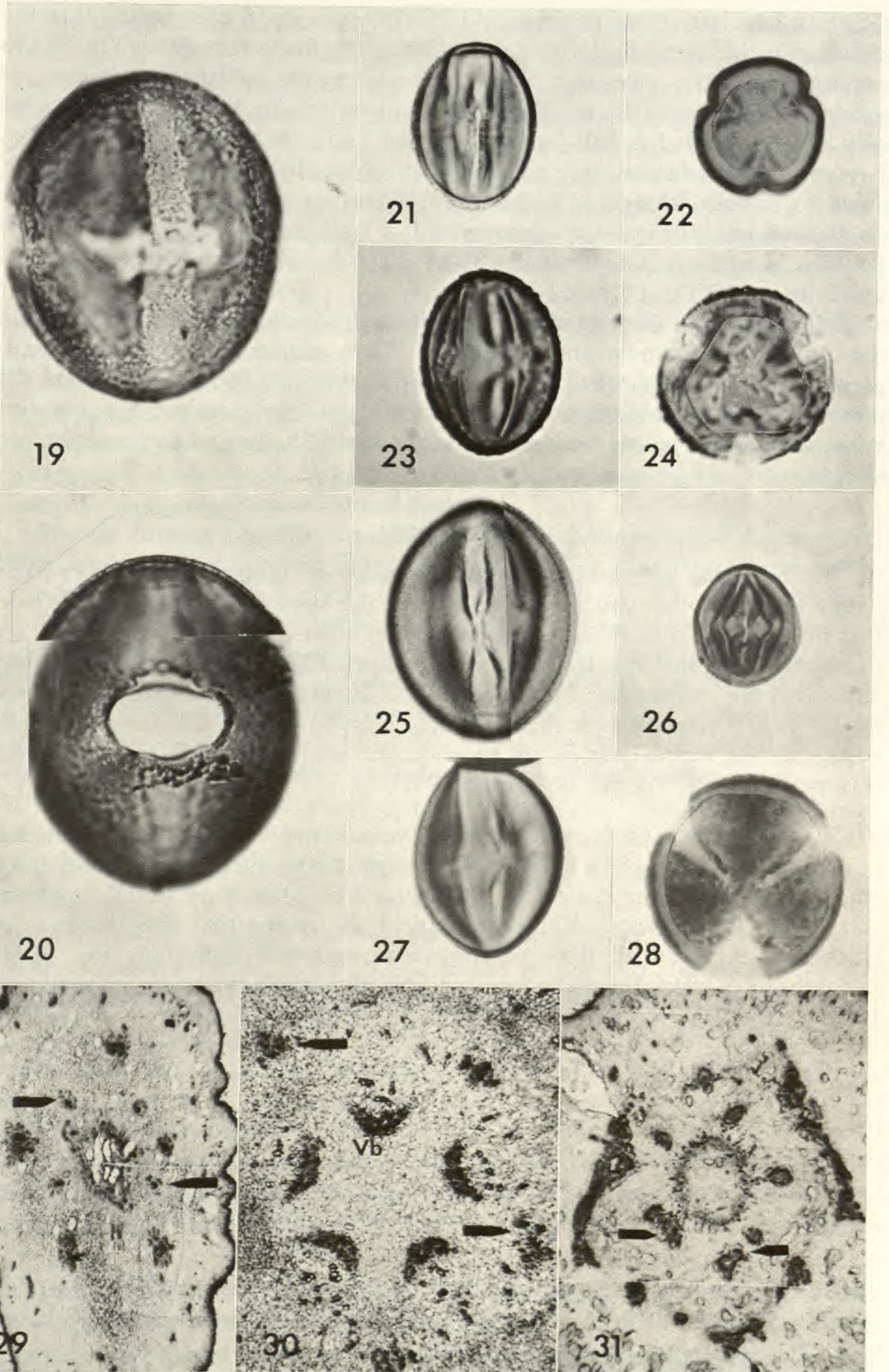
tectate or intectate. Exine thickness 1–1.5 μ. Ektexine equal to or greater than the endexine in thickness. Sculpture: psilate, scabrate, finely reticulate (Fig. 22) to rugulate (Fig. 24). Apertures: zoniaperturate, tricolporoidate, tricolporate, or tricolpate. Colpi are costate. Colpi often appear constricted at the equator or they may be divided in half by an equatorial bridge in the ektexine (Fig. 23). Pore zone often indistinct, appearing as a thin area in the endexine. When present, porae are usually lalongate. Delimitation of the porae is usually diffuse. Size: *Cochlospermum* averages for most species P = 17–23 μ; E = 16–27 μ (*C. gregorii* P = 25 μ; E = 34 μ). *Amoreuxia* P = 33–34 μ; E =32–35 μ (reported as 22 × 19.5 μ by Erdtman, 1952). (Figs. 21–28.)

Pollen grains of *Bixa* examined in this study are easily distinguished from those of *Cochlospermum* and *Amoreuxia*. They are tectate, reticulate, tricolporate with ektexine elements on the colpi membranes (Fig. 19) or around the porae (Fig. 20). The porae are oval, lalongate occasionally with ragged, indeterminate ends. *Bixa* pollen is considerably larger with the longest axis extending to over 40 μ.

Discussion

The flower has been subject to a greater variety of interpretation as to its basic nature than any other structure of the plant. The basic assumption is made here that the flower is a modified shoot, *i.e.* a short stem with specialized lateral appendages. Lengthy evidence has been presented (Eames, 1931, 1961; Moseley, 1961) that the vasculature of the receptacle is homologous with that of the vegetative shoot. Ontogenetic studies by Tepfer (1953) uphold this view. Perianth parts, stamens, and carpels do not appear to be fundamentally different than the leaves of the shoot (Sporne, 1958; Joshi, 1947).

Perianth.—The most primitive perianth vasculature is seen in *Cochlospermum orinocense* and *C. regium* in which five sepal traces alternate with five petal traces in the base of the receptacle. Quincuncial initiation is not usually apparent due to the lack of internodal elongation of the receptacle. Other species of *Cochlospermum* and all those of *Amoreuxia* examined show only five to six perianth traces which branch to form a plexus from which the traces are produced for the calyx and corolla. In all specimens examined, the outermost perianth traces trifurcate and form a plexus whether or not the petals may be supplied separately. The fusion of these traces is probably a natural result of the phylogenetic shortening of the axis to where the phyllotactic spiral disappears completely.

Wilson (1937) accurately illustrated the perianth vasculature for *Cochlospermum vitifolium* as containing six perianth traces for its pentamerous perianth. It is difficult to understand the function of the sixth trace. It is possible that the basic number of perianth traces in the family is 10 and reduction to 5 may be a result of contracted space in the receptacle. Bilateral symmetry of the vasculature is well developed and the sixth trace is probably a vestige of separate petal vascularization. The sixth trace is produced on a side of the receptacle where perianth vasculature is least strongly developed.

Androecium.—In his discussion of the phylogeny of the stamen, Wilson (1937) used several lines of circumstantial evidence to support the hypothesis that stamens are derived from branching systems. He stressed that the Parietales and Malvales provide evidence upholding the telome theory. These two orders contain a number of families which have fascicled stamens or branched stamen trunk bundles in the receptacle, and the Cochlospermaceae were cited as an example. Wilson believed stamen trunk bundles to be relicts of highly branched clusters of sporangium-bearing branches or fertile telomes. In *Cochlospermum vitifolium* five gaps in the stele produce three single trunks, one double trunk, and one triple trunk (Fig. 31). The precocious branching in the latter two cases cannot be considered dichotomous branching, a condition cited as the anatomical basis for primitive telome formation.

Eames (1961) agreed that the existence of trunk vascular supplies would seem to support the view that the fascicle is a unit organ but that actually the formation of fascicles is probably an early step in androecium reduction. Basing his views on comparative anatomy of Dilleniaceae and Paeoniaceae, Eames held that the fascicle is an aggregation of simple stamens.

Neither concept adequately explains the nature of stamen trunk bundles nor do they consider developmental data. In many families, floral vasculature reflects a history of separateness for many presently fused parts. Wilson's concept would require regarding malvalian genera with visible fascicles as primitive, those with numerous stamens and vascular trunk bundles in the receptacle (Cochlospermaceae, Bixaceae, Cistaceae) as intermediate, and laminar stamens with separate traces (Magnoliaceae, Degeneriaceae) as most specialized. Clearly, this concept does not agree with other lines of comparative anatomical evidence (Bailey, 1944, 1951; Bailey & Swamy, 1951; Canright, 1952). Wilson (1965) concluded that reduction in the number of stamens per trunk bundle and reduction in the number of trunk bundles has been the case in *Hibbertia* (Dilleniaceae). While this is probably the case for that genus, there is no reason to regard this as a unidirectional sequence. Selection pressure on the pollination system could prolong the activity of the androecial meristem. The genus *Bixa*, many ways more specialized than Cochlospermaceae, including its anther morphology, has nearly twice as many stamens as any species of *Amoreuxia* or *Cochlospermum*.

There is as great a difficulty in explaining the stamens as aggregates as there is with telomes. To consider the stamens as aggregates, it must be assumed that vascular fusion preceded the aggregation of anthers. Presently accepted tenets of floral evolution agree that fusion of parts is a specialized condition, and such specialization is almost universally reported to precede vascular fusion. The stamen trunks are related to single gaps and show no evidence of any major reorganization at the stele of the receptacle. The genera showing stamen trunks (*cf.* Corner, 1946; Sporne, 1958) all have a shortened receptacle with a laterally expanded torus, a condition which removes the space where spiral phyllotaxis might otherwise occur. When shortening of the floral axis occurs in strobiloid flowers, crowding of the vasculature produces a complicated plexus of anastomosing traces as in *Nymphaea* (Moseley, 1961) and *Nuphar* (Moseley, 1965).

Vascular fusion in these genera is quite different from those in which stamen trunk bundles are found.

Difficulties presented by the telome and aggregation theories are eliminated by the centrifugal stamen concept as revived by Corner (1946) from original observations by Payer (1857). Corner accumulated developmental evidence showing that the broad disc from which the stamens arise is the last portion of the floral apex to develop. Using the genera *Wormia*, *Tetracera*, and *Bixa*, Corner showed that the stamen primordia arise radially from the base of the gynoecium separating it from the already well-developed perianth primordia. This disc interposes tissue in a centrifugal direction (basipetal with reference to the gynoecium). A provascular zone, beginning as five traces, branches regularly to produce well spaced rows of traces and stamen primordia. One implication of this developmental pattern is that numerous stamens may be specialized over few, a trend opposite to that in strobiloid flowers. Centrifugal development probably arose early in angiosperm evolution, but it is not known if it developed out of or concomitant with the strobiloid androecium. No indication of the origin of centrifugal stamens has appeared in genera thus far shown to have the condition. However, an intensive investigation from a developmental standpoint might prove to be highly informative.

Gynoecium.—The ovary structure of Cochlospermaceae has been subject to misinterpretations of important systematic consequence which could have been avoided by serial sectioning. Eichler (1871) described the ovary of *Cochlospermum* as having three to five placentae with a septum dividing the ovary from base to apex into three to five locules. Pulle (1906) described a three-chambered ovary in *C. wentii*. On the other hand, Pilger (1925) and Hutchinson (1967) separated *Cochlospermum* and *Amoreuxia* by the presence of a single chambered ovary in the former in contrast to a multichambered one in the latter. All material I examined had a single ramified locule in the ovary. Transections cut low or high appear axile while those at the center appear parietal. Both genera are identical in this respect.

Description of the gynoecium of *Cochlospermum orinocense* by Schnarf (1931) was based on serial sections, but he made no mention of the position of vascular bundles. In speculating on the nature of the gynoecium, he felt that his material provided no evidence as to whether the septa were laminal outgrowths of the ovary wall or the united walls of carpels. He concluded that we can probably assume they are not united carpel walls. Hutchinson (1959) illustrated the gynoecium of *C. tinctorium* as having marginally joined carpels with a single circular locule. No specimen studied here approximated his drawing. If we assume that the presence of pairs of vascular bundles running up the lamina of the ovary are ventral carpel bundles, then certainly the laminae are fused carpel walls and not secondary proliferations or septae.

Several authors have discussed the evolutionary status of axile versus parietal placentation (Parkin, 1955; Puri, 1952; Eames, 1961). Arguments distinguishing between primitive parietal and advanced parietal placentation seem unconvincing. All such discussions seem to assume that carpels were completely closed or com-

pletely open when syncarpy took place. Gundersen (1939) has pointed out that *Hypericum, Theobroma, Shortia, Feijoa,* and *Myrtus* have ovaries which have axile placentation in the base of the ovary and parietal placentation in the upper part. There is no basis to assume that those ovaries were originally all closed or all open before syncarpy took place. Gundersen noted that wherever there is a change in placentation in ontogeny, it is always from parietal to axile. His opinion on the primitiveness of parietal placentation is thus based on recapitulationary arguments. There is no evidence for determining whether the partially parietal placentation in the Cochlospermaceae is primitively axile or primitively parietal or whether the carpels were partially sealed at syncarpy. In Puri's (1952) comprehensive review of the nature of the placenta, he is not sure that the primitively parietal condition actually exists. The condition is held by him to be derived from axile placentation in a number of families. In descriptive work, the terms axile and parietal should be used topographically without trends of specialization being necessarily implied.

Level of specialization in the flower.—In both genera, primitive features include hypogenous structure, separate perianth parts, separate stamens, numerous ovules. Of intermediate specialization can be included open racemose inflorescence, centrifugal stamen maturation, numerous stamens, expanded receptacle, incipient bilateral symmetry, poricidal dehiscence of the anther, and the syncarpous gynoecium. The flowers of the family can be best characterized as between primitive and moderately specialized.

Relationships among the Parietales and Malvales.—*Bixa* is undoubtedly related to the Cochlospermaceae but is more specialized in many ways including the more numerous stamens, folded anthers with apical (morphologically lateral) dehiscence (Venkatsh, 1956), and reduction of the gynoecium to two carpels. *Bixa* is more primitive in having no detectable bilateral symmetry and in having separate calyx and corolla vasculature. Trichomes on the ovary wall are vascularized by the dorsal wall vasculature. *Bixa* has been separated biologically from *Amoreuxia* and *Cochlospermum* for a very long time, and its placement in a separate family seems justified. The evidence from vegetative anatomy supports this view.

Flowers of *Rhopalocarpus* are readily distinguishable from the above genera by the four-merous perianth, fewer and larger ovules, an androgynophore, as well as numerous gross differences in vegetative anatomy. Its inclusion with *Dialyceras* in the Rhopalocarpaceae by Capuron (1962) is upheld by the studies of Huard (1965a, b, c).

The Flacourtiaceae, thought to be the basal stock from which the Bixales (Cistales) series arose, are poorly known at present. Evolutionary tendencies in this family have produced perigyny, epigyny, loss of petals, unisexual flowers, reduction in stamen number, and reduction in carpel number (Cronquist, 1968). The genera of flacourts with which the Cochlospermaceae show closest affinities is yet to be identified.

Many features found in the flowers of the Cochlospermaceae seem to be widespread in both parietalian and malvalian families. Trifurcating sepal traces with separate petal bundles are common in many families including the Cistaceae

(Saunders, 1936), the Sterculiaceae (Rao, 1949), Tamaricaceae (Murty, 1954), and the Bixaceae. The Rhopalocarpaceae (Huard, 1965a) have separate petal and sepal traces with an indefinite number of parallel traces arising from a single gap for each appendage. The formation of a plexus or ring from which the petal traces arise is also found in the Onagraceae (Baehni & Bonner, 1948) and the Dilleniaceae (Wilson, 1965).

Corner (1946), Sporne (1958), and Wilson (1937) have listed the families which have stamen trunk bundles as follows: Actinidiaceae, Aizoaceae, Bixaceae, Bombacaceae, Cactaceae, Capparidaceae, Crossosomataceae, Cochlospermaceae, Dilleniaceae, Flacourtiaceae, Hypericaceae, Lecythidaceae, Malvaceae, Onagraceae, Loasaceae, Paeoniaceae, Theaceae, and Tiliaceae. A characteristic of this type of stamen vasculature is almost complete separation of androecial and perianth vasculature. This is well illustrated by *Sparmannia* (Tiliaceae) figured by Sporne (1948).

Of the families listed above, malvalian flowers have the most highly advanced centrifugal stamens with their clusters above the receptacle, staminal tubes, or fusions to the style. Cochlospermaceae have not reached that level nor have many other genera associated with malvalian families. The imbricate calyx of the Cochlospermaceae and Bixaceae might seem to preclude inclusion in the Malvales, but the valvate condition is easily derived from the imbricate. *Ryania* (Flacourtiaceae) shows the transition from an imbricate to a valvate calyx in each flower. Nor does parietal placentation really present a difficulty. In the Tiliaceae, the genera *Belotia, Christiania, Colona, Entelia, Goethalsia, Mollia, Nettoa, Sparmannia, Tilia,* and *Triumfetta* all have parietal placentation appearing in at least some sections of the ovary (Weibel, 1945; Baehni, 1934). Several of the genera have ovary morphology almost identical to that of *Amoreuxia* and *Cochlospermum.*

A comparison of pollen characters demonstrated that almost all families of the Bixales, Theales, and Malvales include tricolpor(oid)ate, zoniaperturate pollen. Their grains have mostly thin exines, psilate to reticulate sculpturing, range from oblate to prolate, and are intectate to tectate (Erdtman, 1952, 1969). Elaborations occur as in the highly sculptured large grains of many genera in the Malvales.

Pollen of the Cochlospermaceae does not closely resemble that of *Bixa* but is distinguished by smaller size and less distinct porae. Many genera of the Flacourtiaceae, Aizoaceae, Ochnaceae, Loasaceae, Tiliaceae, Sterculiaceae, and Theaceae have pollen close to that of the Cochlospermaceae, when all characters are considered.

None of the other families in the Bixales or Theales have more than a few random characters in common with the Cochlospermaceae and Bixaceae. I suggest that the Cochlospermaceae and Bixaceae are transitional families. Their level of specialization would be considered primitive for the Malvales, yet they seem unquestionably allied to them. We can agree with Meeuse (1965), who placed the Flacourtiaceae and Dilleniaceae as basal families of this taxonomic plexus, that the relationships of the many families will be difficult to clarify.

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